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## Diceros bicornis. By A. K. Kes Hillman-Smith and Colin P. Groves

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### Diceros Gray, 1821

*Diceros* Gray, 1821:306. Type species *Rhinoceros bicornis* Linnaeus, 1758, by monotypy.

*Opsiceros* Gloger, 1841:125, xxxii. Type species *Rhinoceros bicornis* Linnaeus, 1758, by subsequent designation (Thomas, 1911).

*Rhinaster* Gray, in Gerrard, 1862:282. Type species *Rhinoceros bicornis* Linnaeus, 1758, by subsequent designation (Palmer, 1904:605). Not *Rhinaster* Wagler (Mammalia, Insectivora).

*Keitloa* Gray, 1868:1025. Type species *Rhinoceros keitloa* Smith, 1836, by monotypy. Proposed as a subgenus of *Rhinaster* Gray, 1862.

*Colobognathus* Brandt, 1878:51. Type species *Rhinoceros bicornis* Linnaeus, 1758. Proposed as a subgenus of *Atelodus* Pomel, 1853.

**CONTEXT AND CONTENT.** Order Perissodactyla, Suborder Ceratomorpha, Family Rhinocerotidae, Subfamily Rhinocerotinae, tribe Dicerotini. The tribe contains one other genus, *Ceratherium*. The genus contains one extant species, *D. bicornis*.

### Diceros bicornis (Linnaeus, 1758)

#### Black Rhinoceros

*Rhinoceros bicornis* Linnaeus, 1758:56. Type locality "India"; corrected to the Cape of Good Hope, South Africa (Thomas, 1911:144).

*Rhinoceros africanus* Blumenbach, 1797:126. Type locality "Cape of Good Hope."

*Rhinoceros keitloa* Smith, 1836:44. Type locality "Mafeking, Transvaal," South Africa; Skead (1973) says Zeerust District.

*Rhinoceros gordoni* Lesson, 1842:159. As "variety" of *R. bicornis*. Type locality, "Sources of Gamka River, Cape Province," South Africa.

*Rhinoceros brucii* Lesson, 1842:159. Type locality "Bahr Homran, Ethiopia."

*Rhinoceros niger* Schinz, 1845:335. Type locality "Africa meridionale partibus interioribus": Chuntop River (=Tsondab, 24.00°S, 15.30–16.30°E, Kuiseb district, Namibia: *fide* Zukowsky, 1965:50).

*Rhinoceros Camperi* Schinz, 1845:335. "ad promotoriem Bonae Spei." (Not *Rhinoceros camperi* Jardine, 1836 = *Rhinoceros sondaicus* Desmarest, 1822.)

*Rhinoceros bicornis major* Drummond, 1876:109. "From the Transvaal to the Zambesi." Restricted to Zululand (see Zukowsky, 1965:39). Zukowsky, in his capacity as First Reviser, gives minor precedence over *major*.

*Rhinoceros bicornis minor* Drummond, 1876:109. "From the Black Umfolosi River up towards Limpopo." Restricted to Zululand (Zukowsky, 1965:39). Zukowsky, in his capacity as First Reviser, gives this name precedence over *major* Drummond.

*Atelodus bicornis*, varieties *plesioceros*, *porrhoceros* and *platyceros* Brandt, 1878:51. No localities given; discussed by Rookmaaker (1983b).

*Rhinoceros bicornis holmwoodi* Slater, 1893:517. Type locality "Udulia, situated at the N.E. point of Usukuma, 50 miles S. of Speke Gulf," Tanzania.

*Rhinoceros bicornis somaliensis* Potocki, 1900:82. "Berbera," Somalia (see Zukowsky, 1965).

*Opsiceros occidentalis* Zukowsky, 1922:162. Type locality "Kao-koveld, Namibia."

*Diceros bicornis punyana* Potter, 1947:385. Type locality "Hluhluwe Game Reserve, Zululand, South Africa." (Meester et al. [1986] attribute this name in error to "Potter & Mitchell.")

*Diceros bicornis longipes* Zukowsky, 1949:16. Type locality "Mogram, Chad."

*Diceros bicornis angolensis* Zukowsky, 1965:73. Type locality "Viru Waterhole, Mossamedes District, Huila Province, Southern Angola."

*Diceros bicornis chobiensis* Zukowsky, 1965:79. Type locality "Konsumbia, sources of the Loma, right tributary of the Kuan-do," Angola.

*Diceros bicornis michaeli* Zukowsky, 1965:115. Type locality "between Engaruka and Serengeti" [Tanzania].

*Diceros bicornis rendilis* Zukowsky, 1965:122. Type locality "Northern Guasso Nyiro" [Kenya].

*Diceros bicornis ladoensis* Zukowsky, 1965:124. Type locality "Lado Enclave" [=Lado region, southern Sudan]. Unavailable (Mertens, 1966).

*Diceros bicornis atbarensis* Zukowsky, 1965:141. Type locality "Anseba Valley, Erythraea" [=Eritrea].

*Diceros bicornis ladoensis* Groves, 1967:274. First available usage. *Rhinoceros kulumane* Player, 1972:29. Hluhluwe Game Reserve, South Africa. Nomen nudum.

**CONTEXT AND CONTENT.** Context as above. Recent works include 2–16 subspecies (Groves, 1967; Harper, 1945; Hopwood, 1939; Zukowsky, 1965). The following seven subspecies are recognized by Groves (1967):

*D. b. bicornis* (Linnaeus, 1758:56, see above). (*africanus* Blumenbach, *camperi* Schinz, *gordoni* Lesson, *keitloa* Smith, *niger* Schinz, are synonyms.)

*D. b. brucii* (Lesson, 1840), see above. (*atbarensis* Zukowsky, *palustris* Benzoni, *somaliensis* Potocki are synonyms.)

*D. b. chobiensis* Zukowsky, 1965, see above.

*D. b. ladoensis* Zukowsky, 1965, see above.

*D. b. longipes* Zukowsky, 1949, see above.

*D. b. michaeli* Zukowsky, 1965, see above. (*rendilis* Zukowsky is a synonym.)

*D. b. minor* (Drummond, 1876), see above. (*angolensis* Zukowsky, *holmwoodi* Slater, *major* Drummond, *nyasae* Zukowsky, *occidentalis* Zukowsky, *punyana* Potter, *rowumae* Zukowsky are synonyms.)

**DIAGNOSIS.** *Diceros bicornis* (Fig. 1) is a dicerotine rhinoceros with anterior dentition absent or rudimentary, and occipital crest protruding posteriorly. The jaws and nasals abruptly end not far in front of the level of the anterior premolars; the mandibular



FIG. 1. *Diceros bicornis* in Nairobi National Park; subadult male and young.



FIG. 2. Dorsal, ventral, and lateral views of the cranium, and lateral view of the mandible of *Diceros bicornis michaeli* (adult male, United States National Museum 199068) from the Tana River, Kenya. Greatest length of cranium is 500 mm. Photograph courtesy D. Fisher, United States National Museum, Washington, D.C., U.S.A.

symphysis is narrow; the ascending ramus of the mandible is somewhat slanting; and there is no marked gonial angulation (Fig. 2). Cheekteeth are brachydont, with protoloph and metaloph at right angles to ectoloph; the crowns lack cement. There is no antecinal vertebra; the dorsal outline of the body is lightly concave, with no marked presacral eminence (Fig. 1). The nostrils are rounded; the eye is situated under the frontal horn; the ears are well-separated on the head and rounded. There is no nuchal muscular hypertrophy. The body folds are less developed than in the Rhinocerotinae, but more than in *Ceratotherium*. The costal grooves are prominent especially in older individuals. The penile prepuce is dark with no eccrine glands and the processus glandis are upstanding flanges attached to the sides of the glans. The upper lip is narrow, elongated and pointed and the lower lip is somewhat extensible. The nasal horn

has a broad, rounded basal portion and a comparatively slender, backcurved stem; the frontal horn is relatively large, its basal portion nearly or completely meeting that of the nasal horn.

The black rhinoceros is easily distinguished in the field from *Ceratotherium* by its shorter head, pointed upper lip, sway-back, and absence of a nuchal hump (Fig. 1). The nasal horn is distinguishable from that of the white rhinoceros (*Ceratotherium*) by its more rounded anterior contour, especially at the base.

**GENERAL CHARACTERS.** Variation among subspecies exists for length of head and body, 280–290 cm; height of body, 132–180 cm; girth given in one specimen as 406 cm (Zukowsky, 1965); and body mass 2,199–2,896 kg (Guggisberg, 1966). However, von La Chevallerie (1970) gives means for body mass of 854.6 kg for eight males and 886.8 kg for six females from Hluhluwe, and 1,124.4 kg for 11 males and 1,080.5 kg for five females from Kenya. Denney (1969) gives similarly small body masses. The record length of the nose horn is 135.9 cm. Horns are longer in females in general with the posterior horn being relatively larger in females than in males in Kenya [length of nasal horn =  $2.00 \times$  length of frontal horn + 7.44 ( $r = 0.804$ ) in males, but  $0.98 \times$  length of frontal horn + 14.34 ( $r = 0.655$ ) in females (Freeman and King, 1969)]. The record length of the frontal horn is 81.6 cm obtained from a specimen of the common Keitloa variety with frontal horn longer than nasal (Best et al., 1962). Desert rhinoceroses, *D. b. minor* from northern Namibia, often have very long frontal horns, sometimes at least as long as the nasal (B. Loutit, pers. comm.). Occasional individuals with long horns, such as in Amboseli, Kenya, have horns in which the basal portion only is upright, the stem points forwards, and the tip turns slightly up again. Three-horned and five-horned specimens are known (Guggisberg, 1966; Neuville, 1927). Mean mass of horns collected in Tsavo, Kenya, between 1964 and 1973 was 1.84 kg giving a mean mass per rhinoceros of 3.68 kg (I. Parker, in litt.). The relations between various body measurements are:  $\log$  body mass (kg) =  $3.122 \log$  body length (m) + 1.593,  $r = 0.966$ ;  $\log$  body mass =  $3.87 \log$  of the diameter of the forefoot (cm) + 1.61,  $r = 0.726$  (Freeman and King, 1969).

**DISTRIBUTION.** The black rhinoceros was originally distributed more or less continuously from Zululand to Somalia (Fig. 3; Sidney, 1965). In Angola *D. bicornis* has always been restricted to the southern part; in Namibia it occurs from Kaokoveld and again (discontinuously) from Caprivi; it was once numerous in Ngamiland and the Shashi river district, but did not occur elsewhere in Botswana. In Tanzania, it was always absent from the high plateau and from the southern shores of Lake Tanganyika. In Somalia, it never occurred within 160 km of Berbera (Funaioli and Simonetta, 1966), although the neotype of *D. b. somaliensis* supposedly comes from near Berbera (Zukowsky, 1965). In the Sudan, a century ago it lived on the Eritrean border and as far north as Roseires, Gallabat, and El Damer (17.35°N). In Zaire, it occurred in Shaba as far north as the Lualaba-Luapula confluence and slightly to the north; until recently also in northeastern Uele district. It lived in eastern Rwanda, and in eastern and northern Uganda, but not in the west and south; it once occurred in Ankole (Guggisberg, 1966). The giant South African race, which became extinct 100 years ago, lived in southern and western Cape Province, and extended northward into Namibia. Beyond this continuous area of distribution, the black rhinoceros extended west of the Nile River in suitable areas: in the Sudan, in the Wau district (7.43°N, 28°E) and south of Lake Keilale (100°N, 29°E); along the Bahr-el-Arab tributaries into the Central African Republic (Owen, 1947; Schomber, 1963); in 1915, in the Rumbek District (Larken, 1947). The distinctive small, long-legged *D. b. longipes* occurred as far southeast as Fort Crampel, Central African Republic, and west into the Ngaoundere District of Cameroun, north to the Lake Chad District and northeastern Nigeria. Further west, there are uncertain reports of black rhinoceroses from Niamey, the northern Ivory Coast, and northern Liberia. The species always may have been localized for habitat reasons: in Zimbabwe there are isolated populations in the Kariba, Mt. Darwin, and Save districts; and in Zambia (Ansley, 1959), there are no records of it in Kabombo, Mwinilunga, Solwezi, western Balovale, or Kalabo. In part, some of the sporadic occurrence may reflect the former presence of white rhinoceroses, since in the Sudan the two species seem to be vicarious. Possibly this was the case in southern Africa also, according to dominant vegetation type. It now remains almost exclusively in conservation areas where the degree of protection has been sufficient to counteract a proportion of the poaching (Fig. 3).

**FOSSIL RECORD.** The genus *Diceros* is known from the upper Miocene of Europe (*D. pachygnathus* or *D. neumayri*) and North Africa (*D. douariensis*, *D. primaevus*—Geraads, 1986; Guérin, 1966; Thenius, 1952). Fossil remains of the extant species are known from Makapansgat (lower Pleistocene or upper Pliocene—Hooijer, 1958) and Hopefield (upper Pleistocene—Hooijer and Singer, 1960). A larger-toothed, less-hypsodont form occurs at Omo (upper Pliocene). The species does not appear at Olduvai until upper Bed II (ca.  $1.2 \times 10^6$  years ago), although *Ceratotherium* occurs throughout (Hooijer, 1969).

**FORM.** The skin is 13-mm thick on the hind parts, where thickest, but is harder and more callous on the soles than elsewhere (de Bouveignes, 1953). The skin is hairless externally in adults, but rudimentary hairs are present in follicles. Arrectores pilorum are absent and large apocrine sweat glands are present (Cave and Aumonier, 1965). There are hairs on the penile skin, but none on the shoulder skin of a fetus and abdominal skin of a juvenile. The abundant apocrine glands are surrounded by highly vascularized myoepithelial cells. The stratum corneum of a juvenile was 100- $\mu$  thick and the stratum Malpighii was 18.5- $\mu$  thick (Cave, 1969).

The anterior horn may be wrenched off, wholly or partially; if partially, a new horn begins to grow (after ca. 5 weeks), underneath, and the older fibers are not naturally severed (Jacobi, 1957). In the completely shed horn, regrowth occurs at a rate of about 5 cm/year, always with a clear demarcation between inner and outer sets of fibers (Bigalke, 1945).

There are two inguinal mammae. Fat content of milk remains at 0.45% throughout most of lactation, but other elements change from colostrum to milk proper: lactose increases from 4.38 to 6.90%; protein decreases from 6.4 to 1.65%; biotin, vitamin B12, and pantothenate vary; riboflavin decreases; vitamin B6 and thiamine decrease at first, then increase (Greider, 1960; Gregory et al., 1965). At 19 months after birth, the milk contains (in percent) only a trace of fat, 8.10 solids, 1.11 casein, 0.34 ash, 0.06 calcium, 0.04 phosphorus, 0.04 sodium, 0.09 potassium, 0.08 chlorides, and trace amounts of vitamins (Greider, 1960).

The skull is less markedly dolichocranial than *Ceratotherium*, but the occipital crest is still markedly produced backwards (Fig. 2). The nasals are steep, humped, and abbreviated in front like the premaxillae. There is a broad rugose area on the frontals for support of the posterior horn. The subaural channel remains open throughout life. The mandible has an abbreviated, narrow symphysis; the corpus is robust and heavy; there is no angular prominence; and the ascending ramus is somewhat slanted. The infraorbital foramen, situated over P3, is often bifid in southern populations, and sometimes in *D. b. brucii* and *D. b. longipes*, but never in East Africa. The antorbital process is mastoid in form; the lacrimal bridge is osseous in 77% of skulls (Cave, 1965).

The premolar row occupies 39–45% of the whole toothrow. The height of unworn molar crowns is 45–55 mm; a crista is nearly always absent from the molars, but is present on the premolars (especially P3 and P4) in *D. b. bicornis*, *D. b. brucii*, and *D. b. longipes*, but not in other subspecies. The crochet is often bifid in *D. b. minor* and other eastern and southern subspecies; medifossettes tend to form on those teeth with cristae; the protoloph and metaloph are at right angles to the ectoloph; the parastyle projects but little; the paracone bulge is less prominent; post fossettes become isolated only late in wear (Rookmaaker and Groves, 1978). The metaflexid is small, its anterior and antero-external walls forming an angle of 100° (Cooke, 1950). Deciduous dentition is described by Hooijer (1958): on DM3 and DM4 the ectoloph has a paracone style, which is absent from DM2, but the mesostyle is slight; there is no metacone style; the anterior cingulum is strong and horizontal, forming a ledge at the base of the protocone; the postsinus is shallower than the medisinus. Permanent P1 typically exists, but may be suppressed by eruption of P2 too far forward. Occasionally, the reverse is true (Schaurte, 1966). Forty percent of a Hluhluwe sample lack p1; almost all other East and South African skulls lack it, only *D. b. brucii* and *D. b. longipes* characteristically retain it (Rookmaaker and Groves, 1978). Occasionally skulls are found with small, cylindrical incisors (Anderson, 1966). Rudimentary mandibular DI1 (canines?) occasionally occur (a case is figured by Schaurte, 1966), but no upper incisors, deciduous or permanent, have been confirmed. Enamel hardness is greater than *Ceratotherium*, 281 kg/mm<sup>2</sup> (Schaurte, 1966). Vialli (1955) records a skull with a right DP4, slightly compressed, rotated through 80°.

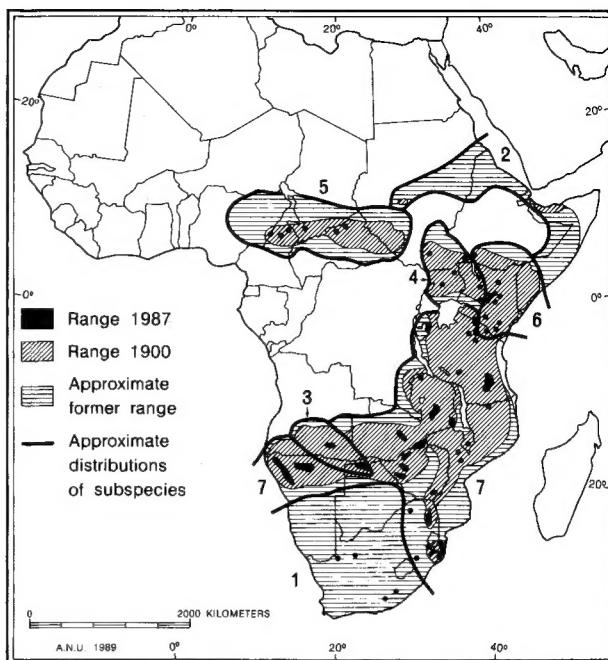


FIG. 3. Current and historic distribution of *Diceros bicornis*: 1, *D. b. bicornis*; 2, *D. b. brucii*; 3, *D. b. chobiensis*; 4, *D. b. ladoensis*; 5, *D. b. longipes*; 6, *D. b. michaeli*; 7, *D. b. minor*.

The brachial index is 84.9; the length of the tibia is 75% of the femur, that of the humerus 96.7% of femur; the length of the tibia is 91.7% of the radius, the length of forelimb is 103.9% of the hindlimb; the length of humerus is 82.8% of the basal skull length, metacarpal III is 46.5% of the radius length; there are subspecies differences in these ratios (Rookmaaker and Groves, 1978). Vertebral formula is 7C, 19–21T, 2–5L (thoracolumbar total 23–24), 4–5S, 21–22Ca (13 skeletons); but an embryo of this species from Punda Milia, Kenya, had 18T, thoracolumbar total 22 (Davies, 1952). Spines of 7C and 1T are elongated, gradually reducing in height from 1T to 7T; spines of 19T to 3L slightly raised; no antecinal vertebra.

In a female from Zambia, the heart weighed 6 kg and measured 305 by 280 mm (Wilson and Edwards, 1965); in two specimens of the nominotypical race it was 460 mm long by 460 mm wide and 340 mm by 340 mm (Rookmaaker and Groves, 1978). The brain of a specimen of *D. b. bicornis* was 16 cm long, 10 cm deep; its volume about one quart (de Bouveignes, 1953). The spleen measured 118–120 by 21–45 cm (Rookmaaker and Groves, 1978). Lungs of a Zambian female weighed 7.3 kg (Wilson and Edwards, 1965); in the Cape specimen they were 61 cm long, and both lobes were subdivided, the right one incompletely (de Bouveignes, 1953). Nasal cavity is large; its membranes very extensive, covering the whole body when unfolded (de Bouveignes, 1953). Viscera amount to 27% of total body mass (Talbot and Talbot, 1961) in an East African specimen and 3.05% when empty, 18.87% when full, in a Zambian animal (Wilson and Edwards, 1965). The esophagus was 91 cm long, the stomach 78.5 by 60.9 cm, the small intestine 11.1 m, the large intestine and caecum 4.5 m, the total being 7 times the head and body length (Wilson and Edwards, 1965) in the Zambian female; in the Cape specimen, the following measurements are quoted by de Bouveignes (1953): stomach, 1.2 by 0.61 m; small intestine, 8.03 m long, 15 cm in diameter; caecum, 1.05 m long, 61 cm at base; colon, 2.44 m long, following course of spine then contracting into a rectum 46 cm long and 15 cm thick. The liver in the Zambian animal (Wilson and Edwards, 1965) weighed 14.5 kg and was 5-lobed, measuring 75 by 50 cm, with no gall bladder; in two Cape animals (de Bouveignes, 1953; Rookmaaker and Groves, 1978) the liver measured 105 by 75 cm and 78 by 60 cm, with three large lobes and one small lobe which was 30 cm long. These rather remarkable differences may reflect adaptations to different environments, or may be purely individual; further studies should be undertaken to estimate ranges of variation in the living populations.

The prepuce is dark; there are no eccrine glands on the penis

(Cave and Aumonier, 1965). Processus glandis are upstanding flanges attached to sides of the glans, with their medial aspects adherent; rounded-triangular in outline; they are curved dorsally, nearly meeting in midline above the glans (Cave, 1964). Kidneys weighed 3.2 kg in the Zambian female, each measuring 23 by 18 cm (Wilson and Edwards, 1965); 45 cm in diameter in the Cape specimen (de Bouveignes, 1953); and about 30 by 19 cm in a captive animal (Meinertz, 1972).

**FUNCTION.** A young male, estimated mass 200 kg, had relatively labile deep body temperature which was considerably influenced by its choice of environment; averaged 38–39.5°C, rising to 40°C after a period of exercise after sunset (Bligh and Harthoorn, 1965). Unstressed specimens had a somewhat lower value, 37.0–37.8°C (Denney, 1969).

The respiration rate averages 22/min, often with a slight catch in the middle of each expiration; after exertion, this rises to 45/min. Respiration falls in rhinoceroses that have been drugged for capture, but the pulse rate does not change (King, 1969). Again, Denney's (1969) figures are somewhat less—respiration 13–18/min in early morning, falling to 7–12/min in the heat of the day.

Pulse rate is 60–92 beats/min (Denney, 1969). There is a rise in respiration, but not in pulse, after being chased (Denney, 1969; King, 1969).

When chased hard, the skin quickly blackens as the dust and dried mud on the skin are soaked with sweat (de Bouveignes, 1953); the function of the apocrine sweat glands is sudden and produced in copious amounts (Cave and Aumonier, 1965).

When it is hot, rhinoceroses drink water daily, though in cold temperatures Thompson (1971) found that they sometimes remained without drinking water for up to 5 days. In arid areas, they also may go without water for some days, obtaining moisture from succulent plants (B. Loutit, in litt.).

Eyesight is poor. Thompson (1971) estimated that effective eyesight extended 25–30 m. Hearing is good. The sense of smell is well developed and probably most important, but its use is limited by wind direction. The liver in six East African specimens contained an average of  $28.7 \pm 3.5$  ppm of copper (Howard, 1964).

**ONTOGENY AND REPRODUCTION.** Estrous cycles occur every 25–30 days (Goddard, 1967). There is no strong evidence of reproductive seasonality. Gestation averages 465 days (range 419–476; Dittrich, 1967; Jarvis, 1967; Yamamoto, 1967); a more recent calculation is 463 days (range 438–480; Ramsay et al., 1987). The female's vulva becomes very swollen from 9 days before parturition. One calf is born. The young have a birth mass of 27–45 kg; for the first 4 months, the average daily mass increase is 1.25 kg. At birth, the nasal horn is just a thickening of skin; at 4 months, it is 4 cm long. The frontal horn begins to appear at 5 months and is 1 cm in length at 6 months (Dittrich, 1967; Jarvis, 1967).

A fetus possessed a pair of genal vibrissae (Cave, 1969). In a 35-mm fetus, however, follicles were traceable over most of the body (Wilson and Edwards, 1965).

Up to about 5 months, the young may be level with or lower than the inguinal region of the female. From 6 months to 1 year it grows to level with the ventral part of the female's vulva. From 1 to 2 years the shoulder becomes level with the tail base of the mother, and by 3 years the young is only slightly smaller than her (Hitchens, 1970).

The placenta is diffuse and villous, as in Equidae, Tapiridae and *Rhinoceros unicornis*. Foliate villi are present as in *R. unicornis*, with villus-free stretches along major vessels (Davies, 1952; Ludwig, 1962).

DM3 erupt by 9 months of age and DM1–4 by 14 months of age (Anderson, 1966); adult M1 erupts at about 3 years (Goddard, 1970a) after which the deciduous premolars are shed (6–7 years—Hitchens, 1978). An individual aged 7 years 3 months had M3 still in process of eruption (Anderson, 1966). M3 usually begins to erupt at >8 years, and is in wear by 11–12 years (Hitchens, 1978). Slightly differing figures are given by Foster (1965): M1 is said to have appeared by 2 years, M2 in 2–4 years, m3 in 4–6 years. Provided allowance is made for individual and inter-population variation and for inexactitude of descriptive language, these figures need not be regarded as conflicting. However, a 14-year-old male in Pretoria zoo had M3 still not completely in occlusion (Schaurte, 1966).

The basal length of young skulls, with full deciduous complement (hence, presumably about 1 year old), is 46–47% of the adult length; females are full sized by the time M2 has erupted, males not until M3 is in wear. Occipitonasal length increases with the gradual prolongation of the occipital crest, its percentage of basal length increasing from 95.2 to 105.0% in the female and 107.0% in the male; zygomatic breadth decreases through the growth phase from 63.6% of basal length when in deciduous dentition to 58.4% as M1 begins to erupt, then increases again to 60–61%; nasal breadth increases steadily throughout growth period.

Age at first mating in captive specimens varies from 4.5 to 9 years, but age at first fertile copulation is from 6 to 9 years (Jarvis, 1967). In the wild, ages of first conception (as well as inter-young intervals) vary between populations, tending to increase in high density populations, or under poor conditions: 3.8–5.7 years in East Africa (Goddard, 1970a); 3.5–4 years in Zimbabwe (Thompson, 1971), but from 3 years 10 months to 9 years 1 month in the high density (introduced) population in Addo N. P., Cape Province: the records for the three oldest ages of first calving (mean, 8 years 11 months) were from the time they were at highest density (Hall-Martin, 1986).

Extreme inter-calf intervals recorded are 24–30 months (Thompson, 1971) and 38–39 months (Mukinya, 1973). The longest intervals in Addo are from the time of poorest conditions; the extremes are 2 years, and 9 years 6 months (Hall-Martin, 1986).

The captive longevity record is 34 years 14 days. Two others survived 30 years, and several survived >20 years in captivity (Reynolds, 1965).

**ECOLOGY.** Black rhinoceroses are found in a wide range of habitats from montane forest, through savanna woodland, bush and thicket, medium grassland–woodland ecotones, scattered tree grassland, and semi-desert, to desert. Medium to dense cover generally is selected, however, especially during the day. In a mixed habitat, A. K. Hillman (pers. comm.) found that 60% of daytime locations of black rhinoceroses were in areas typified by lateral cover of 50% or more. Hitchins (1969) in Hluhluwe Reserve and Thompson (1971) in Zimbabwe found a direct relationship between density of rhinoceroses and density of habitat, with densities  $\leq 1.7/\text{km}^2$  in the thickest habitat in Hluhluwe, which supported 25.7% more black rhinos than the savanna. Goddard (1967) found local densities varying from 0.03 to  $1.3/\text{km}^2$  in Tsavo depending on habitat and  $0.2/\text{km}^2$  in Olduvai with  $0.3/\text{km}^2$  in mixed habitat of Ngorongoro. In the more open Serengeti, Frame (1980) found densities from 0.02 to 0.05/ $\text{km}^2$ .

Black rhinoceroses are browsers on woody shrubs, small trees and certain forbs. Some grass is taken with other things and succulent plants are often selected in the dry season (Mukinya, 1973). Black rhinoceroses have even been observed to select charred twigs after a burn (P. M. Hitchins, pers. comm.). In feeding trials, adult intake averaged 23.6 kg of mixed browse per day (A. K. Hillman, pers. comm.).

Goddard (1968, 1970b) recorded 191 species of plants in Ngorongoro (Tanzania) and 102 in Tsavo (Kenya) eaten by black rhinoceroses, while Hall-Martin et al. (1982) recorded 111 species consumed in Addo (South Africa). Species used vary with area and season, but certain species of *Acacia* and *Dichrostachys* commonly are selected as are nitrogen-fixing legumes. In the extremely arid Damaraland in northern Namibia, Loutit et al. (1987) recorded 74 species of plants browsed by black rhinoceroses, concluding that they use a wide variety of available species and shift food selected according to circumstances, and that they are able to use plants that have heavy chemical defenses against most herbivores.

Black rhinoceroses are predominantly solitary, the most commonly observed groups being lone males, and adult females with young. Females without young usually are alone, but may associate with others. Subadults frequently associate with other black rhinoceroses. An adult male and female, with the latter's young if she has one, form temporary associations for mating during the female's estrus. Other aggregations of various ages and genders occur, but usually are temporary. The largest temporary group reported by Goddard (1970a) was of 13.

Sex ratios vary among populations, but overall are close to 1:1 for all age classes combined. Goddard (1967) found cow:young ratios in Ngorongoro of 1:0.72 and in Olduvai of 1:0.79, with recruitment rates of 7.0% and 7.2%, respectively. In Tsavo, recruitment rate was 10.9% (Goddard, 1970b).

Hyaenas (*Crocuta crocuta*) and lions (*Panthera leo*) are known to prey on young black rhinoceroses and some instances of lions attacking adults are reported (Ritchie, 1963; Thompson, 1971). Goddard (1970a) reports threat behavior by adults towards lions, and an adult killing a lion in defense of her young, but the main predators of adult black rhinoceroses are humans.

Black rhinoceroses often have a symbiotic relationship with oxpeckers (*Buphagus africanus* and *B. erythrorhynchus*). The birds feed on external parasites of the rhinoceroses and with the bird's more acute eyesight give warning of potential danger. Less important and more temporary associations sometimes occur with cattle egrets (*Bubulcus ibis*), starlings (*Lamprotornis*), and drongos (*Dicrurus adsimilis*). Black rhinoceroses occasionally have been observed to associate temporarily with buffalo (*Synacerus caffer*) profiting from the buffalo's more acute vision (Thompson, 1971).

In many areas black rhinoceroses have skin lesions behind the forelegs caused by filarial parasites carried by the fly *Rhinoussa brucei* (Hitchins and Keep, 1970; Sheldrick, 1980). Ticks are common in skin folds, around the anus, eyes and ears. Many black rhinoceroses also have intestinal infestations of the larvae of *Gyrostigma* (C. Dewhurst, pers. comm.). Black rhinoceroses also have blood parasites to which they may succumb if stressed. Anthrax and pernicious anaemia have caused deaths, particularly when black rhinoceroses have been moved to other areas or to captivity (Hillman-Smith, pers. comm.).

As sedentary, easy to stalk animals, populations of black rhinoceroses were severely reduced in the south of the range by early colonial hunters, and the nominotypical *D. b. bicornis* was exterminated; their numbers were also reduced to some extent by conflict with agriculture and loss of habitat. But conservation measures in the 1930s to 1950s, such as the creation of national parks, gave them adequate suitable habitat to support large numbers, until poaching became a major problem. Few indigenous people of Africa placed much traditional value on parts of black rhinoceroses, but a strong pressure to kill them for their horns developed from a demand from the Far and Middle East. Rhinoceros horns were used principally as fever-reducing medicinal agents in the Far East and as a prestigious traditional dagger (Jambia) handle in North Yemen (Martin, 1985). Poaching escalated in the early 1970s, concurrent with, but slightly later than, the rise in ivory poaching. The price of rhinoceros horns rose 2,000% between 1975 and 1979 and the world market then averaged 8 metric tons/year (E. B. Martin, pers. comm.), equivalent to over 2,100 black rhinoceroses/year (A. K. Hillman, pers. comm.).

Experiments have shown that injection of aqueous extract of rhinoceros horn (species not stated) in laboratory rats does, in fact, produce a short-lived antipyretic effect; but horns of cattle and buffalo produce a similar, if less marked, action, and horns of *Saiga tatarica* (Bovidae) give a reaction equal to that of rhinoceroses (But et al., 1990).

In 1969, the black rhinoceros population of Kenya was probably 15,000–20,000 animals. By 1977 there were ca. 2,000–4,000 and in 1979 <1,500, a reduction of 90% in 10 years (Hillman and Martin, 1979); by 1987 the number was 500 (according to the African Elephant and Rhino Specialist Group in 1987). In Tsavo National Park alone, between 1969 and 1979 the black rhinoceros population went from approximately 7,000 to 150 (Hillman, 1983). In 1981, there were estimated to be 10,000–15,000 black rhinoceroses in 18 countries in Africa, but of these only five countries had >1,000 individuals (Hillman-Smith, pers. comm.). All black rhinoceroses were distributed in about 78 populations, but 55% of those contained <50 individuals, a situation where loss of genetic heterozygosity could become a problem. Seventy-four percent of the populations, representing 84% of individuals, were decreasing (Hillman, 1983). In 1984 the estimate was down to 8,800 (Western and Vigne, 1985) and in 1987 to around 3,800 in ca. 69 locations (Cumming and Du Toit, 1989). Black rhinoceroses were known to be present in Tanzania, Zambia, Kenya, Zimbabwe, South Africa, Namibia, Malawi, Rwanda, and Botswana (listed in descending order of their 1980 population sizes), while their numbers or even continued existence in Central African Republic, Sudan, Somalia, Angola, Mozambique, Cameroon, Ethiopia, and Chad were in doubt. (Since then a small population has been reported from Somalia: J. Sale, pers. comm.)

The only countries reporting increases in black rhinoceroses since 1980 were South Africa, Zimbabwe, and Namibia. Since 1971 South Africa has been successfully translocating black rhinoceroses from a high density and increasing population in Umfolozi-Hluhluwe

Game Reserve to other protected areas within their range (Brooks, 1983). In 1987 Zimbabwe contained 1,760 black rhinoceroses, at that time the largest population in any one country, but since then the black rhinoceros in the Zambezi Valley have been subject to severe poaching. In Namibia, poaching of black rhinoceroses in Damaraland in 1989 prompted the first application of the conservation measure of de-horning (Hillman-Smith, pers. comm.).

Since 1979 there has been continual international action to try to slow declines. These have largely been coordinated through Conservation Action Plans drawn up by the African Rhino Specialist Group of the IUCN/SSC (Hillman, pers. comm.), which then became the African Elephant and Rhino Specialist Group (Cumming and Du Toit, 1989; Cumming and Jackson, 1984), and through National Rhino Conservation Strategies, such as those of Kenya and South Africa. In Kenya this has had to include moving black rhinoceroses into fenced and intensively protected sanctuaries, either within existing national parks or on private land. In South Africa most protected areas are already fenced and controlled and detailed plans for management of populations of black rhinoceroses, with strict criteria for movements, are possible (M. Brooks, pers. comm.).

Most countries that traded in rhinoceros horns have now signed the Convention on International Trade in Endangered Species (CITES) and have been taking steps to implement bans on trading (Martin, 1985). However, since 1986, Taiwan, which, through China, is party to CITES, has emerged as a major entrepot with escalating prices and volumes of traded rhinoceros horns (Vigne and Martin, 1989).

It is unlikely that the black rhinoceros will go totally extinct, but their recent decline has been one of the most precipitous of any large mammal. Many populations have been and are being lost as is much of the previous subspecific variation.

In 1981 there were about 169 black rhinoceroses in captivity, with a sex ratio of 1:1.3, but their numbers were declining at about 7%/year (Lindemann, 1983). Steps have been taken towards counteracting the decline and securing back-up populations in captivity. Following the relocation from the Natal Parks Board to zoos and institutions in the USA since 1983, the world captive population was 87 males (38 wild caught, 20 captive born) and 103 females (55 wild, 48 captive born; Lacey, 1987). There were 82 identifiable founders and 49.6 effective founders. Rookmaaker (1983a) attempted to estimate the numbers of each subspecies in the captive stock; only *D. b. minor*, *D. b. michaeli*, and perhaps *D. b. ladaensis* are represented.

**BEHAVIOR.** Black rhinoceroses are sedentary, remaining largely within their own home ranges. Ranges overlap for all except dominant males, and vary in size with habitat and possibly population density. Goddard (1967) found mean ranges (in km<sup>2</sup>) in Ngorongoro (Tanzania) of: adult males 15.6, females 14.9, immature males 35.9, and immature females 27.4, but with ranges as small as 2.6 in forest with water. In poorer habitat at Olduvai (Tanzania), home ranges were larger: 21.8 for males, and 35.1 for females. Home ranges in Mara (Kenya) were 5.6–22.7 (Mukinya, 1973), and were 43–133 in Serengeti (Tanzania—Frame, 1980). In medium to dense habitat black rhinoceroses adopt ranges of 2–17 after introduction, despite the availability of more unoccupied habitat (Hillman-Smith, pers. comm.). In desert habitat, Loutit et al. (1987) found large ranges shared by a number of individuals, for example, 500 used by two females with young and one mature male. Within overall ranges, certain areas may be more frequently used (core areas) and there may be differential use of parts of the range seasonally. Subadults generally have larger ranges than adults, probably as a means of dispersal (Frame, 1980; Goddard, 1967; Loutit et al., 1987; Mukinya, 1973).

As home ranges, even of males, overlap, Goddard (1967) did not recognize territoriality, although he described behavior patterns indicative of territorial defense. P. M. Hitchins (pers. comm.) and Hillman-Smith (pers. comm.) found evidence of similar territoriality to that of the white rhinoceros (*Ceratotherium simum*), that is, dominant alpha males maintaining territories against other dominant males, but allowing overlap by subordinate males and females and subadults. In excessively arid areas, Schenkel and Schenkel-Hulliger (1969) claimed that black rhinoceroses are entirely nomadic, lacking any trace of territoriality or even regular home ranges. Overlapping, but distinct, home ranges were recognized in arid desert of northern Namibia (Loutit et al., 1987).

Black rhinoceroses are more active, both feeding and walking, in early morning and late afternoon to evening. Although Goddard (1967) found a slight rise in activity in the middle of the day, he observed that at 1200 h, 70% of the rhinoceroses were inactive (sleeping or standing). His observations and those of Hillman-Smith (pers. comm.) using radiotelemetry indicate that black rhinoceroses usually are active at night, often feeding, drinking, and walking outside their core areas and in more open habitat than during the day. Resting black rhinoceroses usually lie on the sternum with tails to prevailing wind, but stand now and then.

A semi-prehensile upper lip is used to twist round twigs in feeding. Hillman (pers. comm.) found the usual feeding height is 0–1 m, though they can reach >2 m. Small trees are sometimes pushed down by walking over them to make high branches available. Diameters of twigs bitten off were mainly in the range 3–10 mm, but could be ≤30 mm. This gives a high proportion of woody to green material in the diet (Hillman-Smith, pers. comm.).

Olfactory communication is important. Like other rhinoceros species, black rhinoceroses frequently defecate in dung piles, and the presence of fresh dung on the piles is thought to indicate to other rhinoceroses who was in the area and when. Adults, particularly males, scrape hind feet in dung which may leave scent on their feet. Goddard (1967) found that a male closely followed a dragged trail of his own dung, and on releases of translocated black rhinoceroses it was found that the spreading of its own dung helped to localize a rhinoceros in an area (Hillman, pers. comm.). Adults, particularly males, spray/urinate on bushes and rocks, scrape hind feet in earth, and rub horns in bushes (complex bull ceremony—Schenkel and Schenkel-Hulliger, 1969).

Ritualized postures are part of direct interactions and sounds vary from the quiet mew between mother and young to loud roars and snorts of aggression (Hillman-Smith, pers. comm.). The female-young bond is strong and the young lies or feeds close to its mother. There are instances of mothers leaving young in hiding when they go to waterholes at night (Thompson, 1971). The young follows close behind its mother when she moves off, unlike the white rhinoceros where the young runs in front. If separated, each calls to the other with high-pitched mews and if the young squeals in distress it may attract other black rhinoceroses as well as its mother. The young usually is forced to leave its mother after 2 or 3 years when she has another calf, or sometimes when she is mated. The subadult may, however, later rejoin its mother for temporary periods of association, especially if it is a female.

Two females usually approach each other cautiously, but with little aggression. On contact they may nudge one another with the sides of the head or horn, then usually walk away. The meeting of a male with a female or another male is more likely to be accompanied by aggression, with a stiff-legged, short-step approach, snorting and occasionally head sweeping or horn pushing in the air. Young are sometimes attacked by males, particularly at mating (Hillman-Smith, pers. comm.).

When males meet, aggression may be violent but usually the subordinate or visitor to a territory retreats. The resident may attack with head lowered and ears flattened emitting a screaming groan. The anterior horn is used for clubbing or goring the other animal (Goddard, 1967). Ritualized behavior and knowledge of the social hierarchy usually prevents physical conflict, but during translocations where the social order is disrupted aggression may lead to fighting and deaths. This occurred even between females at Addo National Park (South Africa) and in a holding paddock in Etosha National Park (Namibia), when densities through introductions became too high (Hall-Martin and Penzhorn, 1977).

An association between male and female for mating may continue over several days while the female is in estrus. It may be associated with some aggression and chasing, and fights with other males may occur. The male usually trails the female at first, continually testing her urine. Approaches before the female is ready are usually rebuffed with short charges that send the male off in a tight circle. The male may then approach the female in a stiff-legged shuffle and may sweep the ground with his horn. In instances where the female is lying down he may prod her with his horn until she gets up. He may attempt to mount frequently, but she will not stand still until she is ready. They may remain in copulo for 30 min or longer, with a number of ejaculations during that time. Mating may be repeated several times a day during the period they are together (Hillman-Smith, pers. comm.).

When alarmed, a black rhinoceros will usually run off with its

tail curled, sometimes emitting a series of snorts. If, however, it is only mildly disturbed and cannot identify the disturbance, it may approach, either cautiously or in a rush. Despite their reputation for aggression, most charges by black rhinos are investigatory or a mild threat which is not carried through into an attack. However, if harassed too much, a rhino may charge and inflict damage.

**GENETICS.** A female that died in Philadelphia zoo had a diploid chromosome number of 84, one of the highest recorded in any mammal. There were 1 pair of large and 3 pairs of small metacentrics; 9 pairs of large submetacentrics; and 13 pairs of longer, 16 pairs of shorter acrocentrics. A small pair of acrocentrics had satellites on the long arms. The X chromosome was not identified (Hungerford et al., 1967). Heinchen (1969) and Ryder et al. (1987) confirm the chromosome number. There is some variation in the number of chromosome arms in *D. b. michaeli* due to the presence or absence of heterochromatic small arms, revealed under G-banding. A single individual of *D. b. minor* had heterochromatic small arms of appreciable size only on four chromosomes, a pattern more similar to that of the white rhinoceros (Ryder et al., 1987).

A recurring syndrome seems to be absence of ear pinnae combined with an underdeveloped tail (Guggisberg, 1966). Goddard (1969) records seven males, only one female, with bilateral absence of ear pinnae; the female may have been sired by one of the earless males, whose mother was not earless. Goddard suggests a sex-linked condition. Conversely, an earless calf was seen by Goddard (1969) in Olduvai, where this character had not been previously recorded. Hitchins (1986) reports that of 21 earless black rhinoceroses examined in Hluhluwe and the Hluhluwe-Umflozi corridor, only one had no scars and so could have inherited the condition; he attributed the other cases to attempted predation on calves, especially by hyenas. The three-horned tendency also appears to be genetic, being localized in different parts of Africa (Guggisberg, 1966).

**REMARKS.** In light of the current threat to the species as a whole, it is considered appropriate to reexamine Groves's (1967) arrangement, which was based on an admittedly small sample, using as many specimens as become available. This is now underway on a cooperative basis by the African Elephant and Rhino Specialist Group (Du Toit, 1987).

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